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THE ANTIPREDATOR VOCALIZATIONS OF ADULT EASTERN SCREECH-OWLS

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Abstract.—Adult eastern screech-owls (*Otus asio*) used six different vocalizations (bounce songs, whinny songs, bark calls, bark-screech calls, screech calls, and bill-claps) during trials in which a human approached nest sites or approached and handled nearly-fledged or recently-fledged young. Bounce songs and whinny songs were uttered more frequently during nest defense trials while bark calls, screech calls and bill-claps were uttered more frequently during trials with young owls. We suggest that bounce and whinny songs serve as low-intensity warnings to mates and nestlings. Bark calls consisted of a single, short duration note and appear to serve as warning calls, informing a mate and young of an approaching predator and informing the predator of a willingness to attack. Screech calls were short duration, high volume calls. Most screech calls were given during flights directed at the predator, and may function as a high-intensity warning call. Bark-screech calls appeared intermediate to bark and screech calls, both in structure and function. Most bill-claps were given during flights directed at the predator, often in conjunction with screech calls. We suggest that the combined vocal signal of screech calls and bill-claps represents the highest-intensity vocal warning directed at potential predators by screech-owls.

Key Words: *eastern screech-owl; vocalizations; antipredator; nest defense;* Otus asio.

Vocalizaciones antideoredadoras de individuos adultos de *Otus asio*

Resumen.—Individuos adultos de la especie *Otus asio* usaron seis vocalizaciones diferentes (cantos de bravata, relinchos, llamados de tipo gruñidos o ladridos, mezcia de gruñidos y chillidos, sólo chillidos y golpes de pico) durante ensayos en los que un humano se aproximó a los nidos o aproximó y tomá a los polluelos. Tanto el canto de bravata como los relinchos fueron utilizados con mayor frecuencia durante la defensa del nido, mientras que las demas vocalizaciones fueron frecuentemente utilizadas durante el acercamiento a juveniles. Sugerimos que, tanto la como el relincho, sirven como alertas de baja intensidad para la pareja y los volantones. Los llamados de gruñidos o ladridos, de una simple nota de corta duración, parecen servir para alertar, informando tanto a la pareja como a las crias de la aproximación de un depredador a informando al deprededor de su disposición de ataque. Los chillidos son de corta duración, pero son llamados de alto volumen. La mayoría de los chillidos fueron hechos durante vuelos hacia el depredador y podría corresponder a un llamado de alterta de alta intensidad. Los llamados de chillidos y gruñidos parecen estar en una categoría intermedia entre los llamados de gruñidos y los de chillidos, tanto en estructura como en la función. La mayoría de los golpes de pico fueron realizados durante los vuelos hacia el depredador, a menudo mezclados con llamados de chillidos. Sugerimos que esta ultima combinación de señales vocales representan la alerta de mayor intensidad vocal dirigidas al potencial depredador por parte de *O. asio.*

[Traducción de Ivan Lazo]

The responses of parent birds to an approaching predator may vary considerably, but often include vocalizations, distraction displays, or attacks. Such behaviors may enhance a parent's reproductive success but do entail some survival cost (Montgomerie and Weatherhead 1988). The extent of that cost varies with the type of response. Distraction displays, such as dives and attacks, may be relatively expensive and risky (Andersson et al. 1980, Greig-Smith 1980, Curio and Regelmann 1985, Knight and Temple 1988). In contrast, vocalizing is neither particularly costly nor risky and, as a result, many parent birds respond to approaching predators by vocalizing (Greig-Smith 1980, Bjerke et al. 1985,

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Table 1. Comparison of the whinny songs and bark calls of male and female eastern screech-owls.

	Males[a]		Females[b]		Comparison of Male and Female Vocalizations (Wilcoxon test)	
	Mean	SE[c]	Mean	SE[c]	z	P
Whinny songs						
Duration (sec)	1.12	0.02	1.13	0.05	0.18	0.8577
Minimum frequency[d]	684.5	14.0	688.6	31.9	1.30	0.1923
Maximum frequency[d]	1101.5	16.7	1419.4	61.7	4.13	<0.0001
FMA[e]	940.8	15.4	1080.0	32.9	3.89	<0.0001
Bark calls						
Duration (sec)	0.24	0.06	0.25	0.01	1.11	0.2670
Minimum frequency	749.4	10.9	813.5	9.3	4.52	<0.0001
Maximum frequency	1092.8	11.3	1147.6	13.5	2.07	0.0382
FMA	959.4	9.5	1014.3	10.0	3.47	0.0005

[a] Eight males gave 80 whinny songs and nine males gave 124 bark calls.
[b] Five females gave 35 whinny songs and 136 bark calls.
[c] Standard error.
[d] All frequency measurements in Hertz.
[e] Frequency at maximum amplitude in Hertz.

Veen and Piersma 1986, Knight and Temple 1986, 1988, Weatherhead 1989). Even well-armed parents (i.e., raptors) may respond to potential predators by vocalizing (e.g., Wiklund and Stigh 1983, Andersen 1990).

Adult eastern screech-owls (*Otus asio*) utter a variety of vocalizations in response to potential predators (Sproat 1992, Sproat and Ritchison 1993). We previously examined the nest defense behavior of eastern screech-owls and reported the use of five antipredator vocalizations (Sproat and Ritchison 1993) but did not provide a detailed description of the vocalizations or discuss possible functions. Here we provide such a description and also discuss the possible function(s) of these vocalizations.

Methods

The vocal responses of male and female eastern screech-owls to potential predators approaching nest sites or young were examined during three breeding seasons (1985, 1990 and 1991) at the Central Kentucky Wildlife Management Area, located 17 km southeast of Richmond, Madison County, Kentucky. A detailed description of methods used during the nest defense trials can be found in Sproat and Ritchison (1993). Briefly, eight pairs of radio-tagged screech-owls (N = 4 in 1990 and N = 4 in 1991) were tested repetitively while six pairs (N = 4 in 1990 and N = 2 in 1991) were tested only once. The repetitive pairs were each tested three or four times, with trials conducted at 12–14 d intervals during the approximately eight-week nesting cycle. Two people were involved in each trial, one acting as an observer and the other as the predator. During each trial, the predator spent 8 min at a point 8 m in front of the nest tree, four min at the base of the nest tree, 4 min about halfway between the ground and the cavity (using a ladder), and a final 4 min at the initial location in front of the nest tree.

To obtain additional recordings, we also examined the responses of eight pairs of screech-owls (three in 1985, three in 1990, and two in 1991) to humans just prior to or after fledging of their young. Pairs tested in 1990 and 1991 had also been used for the nest defense trials while those tested in 1985 had not been tested previously. Further, only those pairs tested in 1990 and 1991 were fitted with radiotransmitters. During these nestling/fledgling trials, young were removed from nest cavities or roost sites, tethered to a branch, and approached and handled by a human. These trials varied in duration and during each trial an attempt was made to record all vocalizations uttered by the adults. Because paired owls were sometimes in close proximity during these trials, we were not always able to determine whether the male or female was vocalizing. We also attempted to determine the number of dives (any break in horizontal flight directed at the predator) made by each member of the pair.

During all trials we noted the number and type of vocalizations uttered by parent owls. Vocalizations were recorded by the person acting as the predator using a Uher 4000 Report Monitor tape recorder with a Dan Gibson parabolic microphone. All vocalizations recorded on tape were subsequently analyzed using a Kay Elemetrics Corp. Sonagraph (Model 5500). For each vocalization we determined duration, maximum frequency, minimum frequency, frequency at maximum amplitude (FMA), and, for bounce songs, the number of notes per song.

Multiple comparisons were made using a one-way ANOVA applied to ranks (equivalent to a Kruskal-Wallis test; SAS Institute 1985) while paired comparisons were made using Wilcoxon tests (SAS Institute 1985). Chi-square tests were used to test for non-random distributions. All values are presented as mean ± standard error.

RESULTS

Eastern screech-owls uttered six different vocalizations during the trials: bounce songs, whinny songs, bark calls, bark-screech calls, screech calls, and bill-claps (Fig. 1). Male screech-owls gave all of these vocalizations while females gave all except bounce songs.

Description of Vocalizations. The bounce songs of male screech-owls ($N = 39$ songs by seven individuals) averaged 1.92 ± 0.06 sec in duration and consisted of an average of 25.33 ± 1.03 notes. The mean frequency at maximum amplitude (FMA) was 620.0 ± 6.1 Hz. The bounce songs of males exhibited significant individual variation in number of notes per song ($F_{4,29} = 4.07$, $P = 0.0097$), maximum frequency ($F_{4,29} = 4.13$, $P = 0.0009$), minimum frequency ($F_{4,29} = 4.07$, $P < 0.0001$), and FMA ($F_{4,29} = 5.96$, $P = 0.0013$) but not in duration ($F_{4,29} = 1.52$, $P = 0.222$).

The whinny songs of male ($N = 8$) and female ($N = 6$) screech-owls differed significantly in maximum frequency and FMA but not in duration or minimum frequency (Table 1). Among males, whinny songs differed significantly in duration ($F_{7,72} = 3.95$, $P = 0.001$), maximum ($F_{7,72} = 34.08$, $P < 0.0001$) and minimum ($F_{7,72} = 21.65$, $P < 0.0001$) frequency, and FMA ($F_{7,72} = 34.79$, $P < 0.0001$). Similarly, among females, whinny songs differed significantly in duration ($F_{5,29} = 6.74$, $P = 0.0003$), maximum ($F_{5,29} = 41.65$, $P < 0.0001$) and minimum ($F_{5,29} = 6.71$, $P = 0.0003$) frequency, and FMA ($F_{5,29} = 25.56$, $P < 0.0001$).

Bark calls consisted of a single note that typically exhibited a gradual decline in frequency (Fig. 1). The barks of female screech-owls were significantly higher in frequency than those of males (Table 1). Among males, bark calls exhibited significant individual variation in duration ($F_{9,115} = 4.61$, $P < 0.0001$), maximum ($F_{9,115} = 5.19$, $P < 0.0001$) and minimum ($F_{9,115} = 4.65$, $P < 0.0001$) frequency, and FMA ($F_{9,115} = 5.83$, $P < 0.0001$). Similarly, among females, bark calls exhibited significant individual variation in duration ($F_{4,131} = 5.82$, $P = 0.0002$), maximum ($F_{4,131} = 6.46$, $P < 0.0001$) and minimum ($F_{4,131} = 4.56$, $P = 0.0018$) frequency, and FMA ($F_{4,131} = 6.06$, $P = 0.0002$).

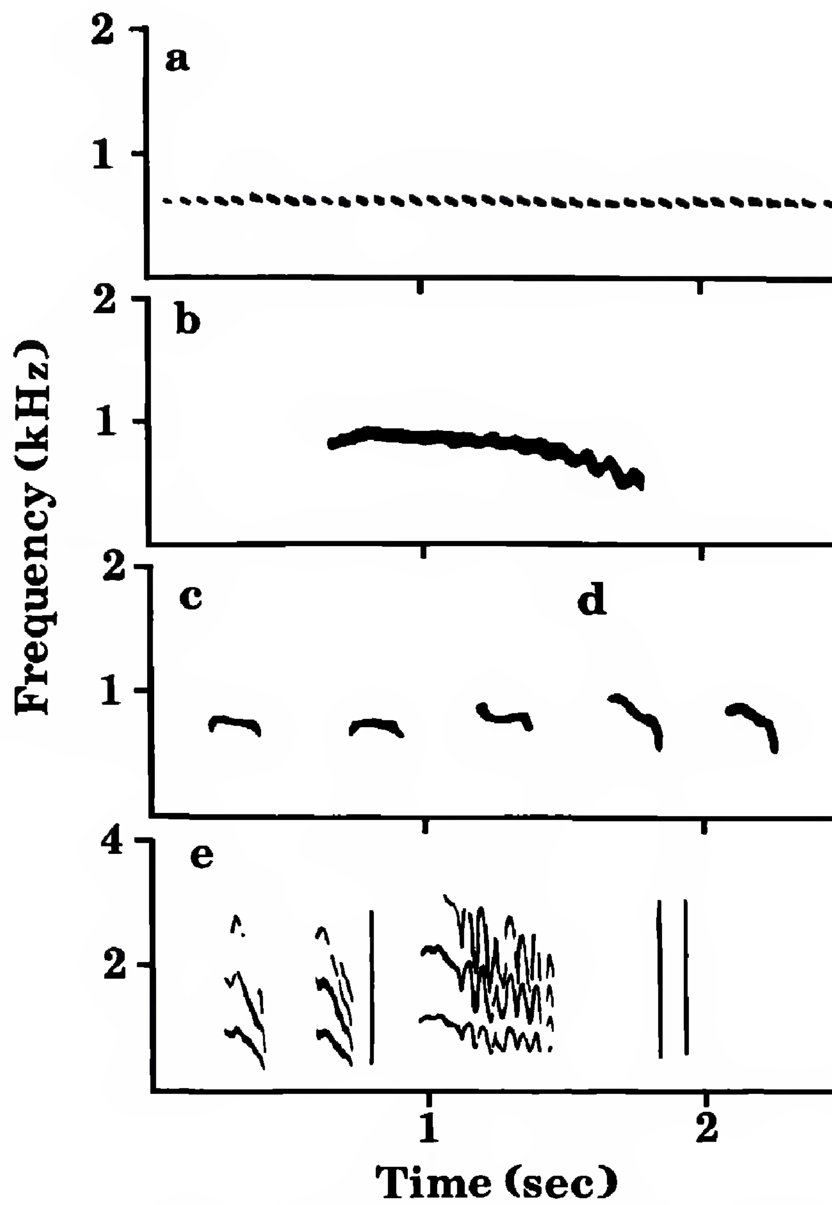

Figure 1. The antipredator vocalizations of eastern screech-owls. (a) bounce song, (b) whinny song, (c) three bark calls, (d) two bark-screech calls, and (e) two screech calls followed by a single bill-clap plus a screech call exhibiting frequency modulation followed by two bill-claps

Bark calls were sometimes given in bouts of two or more (with a bout defined as a series of the same calls with intercall intervals of 30 sec or less). The mean number of bark calls per bout ($N = 71$ bouts by at least 18 individuals) was 6.42 ± 1.01. Females ($N = 6$) gave significantly ($z = 3.21$, $P = 0.0013$) more barks calls per bout than did males ($N = 8$), with males averaging 3.87 ± 0.83 calls per bout and females averaging 5.96 ± 0.86 calls per bout.

Bark-screech calls were uttered by one or both members of one pair of screech-owls during a nestling/fledgling trial, and the characteristics of these calls were intermediate to those of bark and screech calls. Bark-screech calls ($N = 19$) averaged 0.21 ± 0.01 sec in duration and had a mean FMA of 793.2 ± 11.5 Hz. These calls exhibited a sharp drop in frequency, descending from a mean high frequency of 943.2 ± 36.3 Hz to a mean low frequency of 523.7 ± 45.4 Hz.

Screech calls were high volume calls consisting of a single note exhibiting a rapid drop in frequency (Fig. 1). Screech calls sometimes ended with a series of frequency modulations (Fig. 1). Most screech calls were given by owls in flight, often during dives. Screech calls (N = 53) averaged 0.25 ± 0.02 sec in duration and had a mean FMA of 884.7 ± 20.5 Hz. These calls descended from a mean high frequency of 1217.1 ± 24.6 Hz to a mean low frequency of 443.2 ± 17.7 Hz. We were able to positively identify only three of the owls (two females and one male) that uttered these calls and, therefore, could not compare the screech calls of males and females.

Bill-claps produced short duration sounds ($\bar{x}$ = 0.02 ± 0.0004 sec; N = 46 by at least four individuals) that covered a wide range of frequencies (Fig. 1). Although most bill-claps were given immediately before or after bark calls (N = 12) or screech calls (N = 24), three screech-owls gave only bill-claps during dives. When given with other calls, bill-claps were given an average of 0.25 ± 0.15 sec (N = 2) before bark calls, 0.31 ± 0.08 sec (N = 5) before screech calls, 1.36 ± 0.85 sec (N = 7) after bark calls, and 0.17 ± 0.03 sec (N = 13) after screech calls. No significant differences were found between the bill-claps of males and females (Wilcoxon tests, $P > 0.05$). Bill-claps were often given in bouts of two or more. The mean number of bill-claps per bout was 1.63 ± 0.13 (N = 27 bouts by at least four individuals) and the mean duration of these bouts was 0.16 ± 0.03 sec.

Vocal Responses During Nest Defense and Nestling/Fledgling Trials. Few vocalizations were uttered during the incubation stage (N = 19 trials). Female screech-owls (N = 2) vocalized during two trials, with one female giving one whinny song and the other 15 whinny songs. Males (N = 5) vocalized during five trials, with one male giving one whinny song and five bounce songs, a second male giving one bark, and three males giving bounce songs (1, 1, and 16, respectively).

Screech-owls vocalized during 14 of 17 trials conducted during the nestling stage. Bark calls (N = 103 by eight males and two females during eight trials) and whinny songs (N = 94 by eight males and four females during eight trials) were the most frequently used vocalizations during the nestling stage. Screech-owls gave few bounce songs (N = 11 by three males) and screech calls (N = 5 by two males and one female) and no bill-claps. Male screech-owls were more vocal than females, with only males vocalizing during seven trials and both the male and female vocalizing during seven additional trials. In addition, vocalizing males gave more calls, averaging 11.4 bark calls (N = 8 males) and 7.8 whinny songs (N = 8 males). Vocalizing females averaged six bark calls (N = 2 females) and 4.5 whinny songs (N = 4 females).

Vocalizations were uttered by adult male and female screech-owls during seven of eight nestling/fledgling trials. Screech-owls used all six vocalizations during these trials, with bark calls given most frequently. During three of the seven nestling/fledgling trials in which adult screech-owls uttered vocalizations, we were unable to positively identify the source (i.e., adult male or adult female) of some or all of the vocalizations. For the remaining four trials, we found that female screech-owls uttered significantly more (χ^2 = 16.2, df = 3, P = 0.001) bark calls per trial than did males, with females averaging 31 ± 13.3 bark calls and males 8.3 ± 5.9 bark calls.

Among those pairs tested during both types of trials (nest defense and nestling/fledgling), the use of vocalizations during the two trials differed significantly (χ^2 = 47.6, df = 4, $P < 0.0001$). Bark calls, screech calls, and bill-claps were used more frequently during the nestling/fledgling trials while bounce songs and whinny songs were used more frequently during the nest defense trials.

DISCUSSION

Eastern screech-owls in our study uttered bounce and whinny songs in an antipredator context; however, these songs are also used in other contexts (Ritchison et al. 1988, Klatt and Ritchison 1993). Bounce songs given by male screech-owls in our study averaged 25.3 notes. By comparison, bounce songs given in response to playback averaged 32.3 notes (Cavanagh and Ritchison 1987) while those uttered during duets averaged 58.4 notes (Klatt and Ritchison 1993). Thus, our results support the hypothesis that the message conveyed by bounce songs varies with song length—shorter songs conveying increasing levels of aggression (Klatt and Ritchison 1993) or perhaps anxiety. Most bounce songs were given during the incubation period when screech-owls exhibited little nest-defense activity (Sproat and Ritchison 1993). These results suggest that bounce songs were probably directed by males toward their

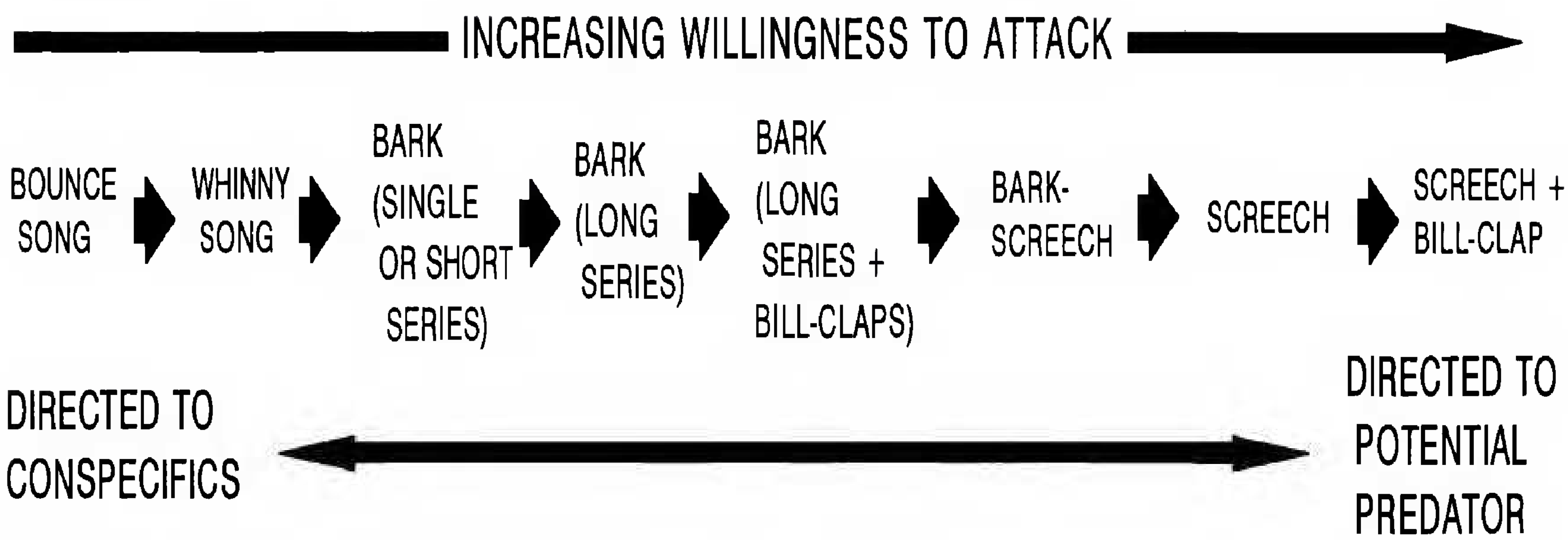

Figure 2. A possible antipredator communication system of adult eastern screech-owls.

incubating mate and served as a low-level warning (Fig. 2).

Screech-owls responded with significantly greater intensity during the nestling stage than during incubation (Sproat and Ritchison 1993), and most whinny songs were given during the nestling stage. Whinny songs are also given with greater volume than bounce songs (Ritchison et al. 1988). This increased volume, plus the association with other antipredator behaviors (e.g., flights and dives), suggests that whinny songs serve as a higher-level warning to mates and nestlings (Fig. 2). The characteristics of whinny songs also make a calling bird relatively easy to locate (Ritchison et al. 1988), suggesting that they may also serve to distract potential predators. Selection should favor the use of easily locatable calls as distraction displays when the caller's position must be revealed (Greig-Smith 1980). Vocalizations that apparently serve to distract predators have been reported in several other species (Greig-Smith 1980, East 1981, Andersen 1990).

Screech-owls in our study also uttered bark calls, bark-screech calls, screech calls, and bill-claps. These calls have been reported previously (Marshall 1967, Walker 1974, Voous 1988, Torre 1990) and are apparently uttered only in aggressive or defensive contexts (Torre 1990). Other species of owls utter similar calls in aggressive contexts. For example, boreal owls (*Aegolius funereus*) utter screech calls when the nest or fledged young are approached by potential predators (Meehan 1980). Bark-like calls have been reported in snowy owls (*Nyctea scandiaca*), little owls (*Athene noctua*), barred owls (*Strix varia*), spotted owls (*S. occidentalis*), and boreal owls (Voous 1988). Bill-claps have also been reported in several species of owls, and are generally uttered in aggressive (including nest protection) or defensive contexts (Johnsgard 1988).

Bark calls were uttered by male and female screech-owls during the nestling stage and, especially, during the nestling/fledgling trials. Our results indicate that bark calls serve to warn a mate and young that a predator is approaching. Kelso (1938:248) reported that when two juvenile screech-owls heard bark calls "... they crouched flat ... and feigned death." Calls with a similar function have been reported in other species (e.g., Greig-Smith 1980, Knight and Temple 1986, 1988, Andersen 1990).

Screech-owls sometimes gave long series of bark calls, particularly during the nestling/fledgling trials. Previous studies suggest that a single call, or a short series of calls, may be sufficient to convey a warning of danger to a mate or young and, further, that a long series of calls are more likely directed at the predator (Powell 1974, Greig-Smith 1980). Our results support this hypothesis. Screech-owls gave relatively short bouts of bark calls during the nest defense trials and these bouts preceded a dive only once, suggesting that the calls were directed at a mate or young. In contrast, the longer series of barks given during the nestling/fledgling trials were often followed by screech calls and dives, suggesting that the calls warn a predator of a screech-owl's increasing willingness to attack (Fig. 2).

Most screech calls were given by screech-owls during flights at the predator, mainly during the nestling/fledgling trials when young were being handled. Kelso (1938:248) observed that screech-owls gave screech calls "... when a person or large animal comes near the young either while they are in or out of the nest. It is usually given as the male swoops at the intruder's head. . . ." The relatively high volume of these calls and the tendency to utter them close to the predator indicate that the calls are directed at the predator and serve as a high-intensity warning (Fig. 2). Bark-screech calls were also given during the nestling/fledgling trials and appeared intermediate to bark calls and screech calls, both in terms of structure and function (Fig. 2).

All bill-claps were given during the nestling/fledgling trials, mainly during flights at the potential predator (often in conjunction with screech calls). As with screech calls, the association of bill-claps with flights at the predator indicates that they are directed at the predator and serve as a high-intensity warning. The combined vocal signal of screech calls and bill-claps may represent the highest-intensity vocal warning given by screech-owls (Fig. 2).

Male screech-owls vocalized more than females during our nest defense trials. Similarly, Sproat and Ritchison (1993) found that male screech-owls defended young in the nest more vigorously than did females. However, female screech-owls vocalized more than males during our nestling/fledgling trials and, in at least two pairs, females made more flights at the predator. Such results suggest that the intensity of defense by female screech-owls may increase when a predator poses a greater threat (i.e., is closer) to the offspring and support the hypothesis that the location of a predator relative to the nest (or fledged young) may influence the defense behavior of male and female raptors that exhibit reversed sexual dimorphism (Sproat and Ritchison 1993).

In summary, eastern screech-owls use several vocalizations in an antipredator context and we suggest that these vocalizations represent a graded system of communication (Fig. 2). Similar graded systems have been reported in other species (Morton and Shalter 1977, Miller 1979, Veen and Piersma 1986, Armstrong 1992), and such systems permit more precise communication because individuals are able to communicate subtle variations in motivation (Morton 1977).

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